

Interspecific odour discrimination in four *Gerbillurus* species

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Abstract

Interspecific odour discrimination was investigated in an attempt to identify possible mechanisms of species recognition in four *Gerbillurus* species. Four-way choice-chamber tests of preference for odours of the opposite sex of *G. paebsi*, *G. tytonis*, *G. setzeri*, and *G. vallinus* were conducted. When test animals were prevented from physically contacting the odour source (soiled sand), males showed more evidence of discrimination than females, but only male *G. tytonis* significantly preferred conspecific odours. Males showed less discrimination among odours of females which had been injected with hormones to induce oestrus.

When test animals were allowed to contact the odour source females showed more evidence of discrimination in two-way and four-way choices. Female *G. tytonis* and *G. vallinus* showed significant preference for conspecific odours in two-way tests.

It is suggested that males responded to a volatile chemosignal of females, but this response diminished if males were permitted to sniff the odour source. Females responded to non-volatile chemosignals deposited by males. However, little evidence for preference of conspecific odours is provided. Physical contact between animals may be necessary for precise species recognition.

Introduction

Olfactory communication is implicated in mate selection, reproduction, territoriality, and parent-offspring interactions in many rodent species (BROWN 1985). The vomeronasal organ, which assists in odour detection, is well developed in rodents (EISENBERG and KLEIMAN 1972), and permits precise discrimination at the level of individuals in some species (JOHNSTON 1982; YOUNG 1988).

Pheromones may be present in urine, faeces and saliva, and also in secretions from glands around the eyes, mouth, genital organs, and skin (BROWN 1985). Sandbathing, which is exhibited by many desert rodents, serves a marking as well as a pelage-dressing function (EISENBERG and KLEIMAN 1972; BROWN 1985). Specific scent-marking behaviour includes perineal dragging and ventral-gland marking in *Meriones unguiculatus* (THIESSEN and HARRIMAN 1983). Harderian gland secretion mixed with saliva is spread over the face during grooming and serves a communication function in *M. unguiculatus* (THIESSEN et al. 1976).

Volatile chemosignals may act as long-distance attractants or territorial indicators, while low-volatile and non-volatile substances may permit acute, short-range identifications which precede sexual and aggressive behaviour (NYBY 1982; BROWN 1985). The odour of an oestrus female mammal has been identified as one of the prime stimuli indicating her condition to the male (EISENBERG and KLEIMAN 1972).

The use of odour differences among closely-related rodent taxa as a means of maintaining reproductive isolation has been investigated in speciating *Spalax ehrenbergi* (NEVO et al. 1976), *Clethrionomys glareolus* (GODFREY 1958), and *Peromyscus* spp. (SMITH 1965; MOORE 1965; DOTY 1972). Preference for conspecific odours was not always exhibited (MOORE 1965), and the oestrus condition of females was important for discrimination in some species (DOTY 1972; NEVO et al. 1976).

In this study, four species of the genus *Gerbillurus* were included in a comparative study of communication in the genus. Preferences for conspecific and heterospecific odours were investigated in a series of experiments based on a choice-chamber technique.

Study species were *G. paeba*, *G. tytonis*, *G. vallinus* and *G. setzeri*. Previous research has shown that *G. paeba* and *G. tytonis* ($2n = 36$) are closely related, while *G. vallinus* and *G. setzeri* ($2n = 60$) are a separate, closely-related species-group (SCHLITTER et al. 1984; DEMPSTER and PERRIN 1989a). Three species, *G. tytonis*, *G. vallinus* and *G. setzeri*, are allopatric, with evidence of occasional and localised overlap in distribution of *G. tytonis* and *G. setzeri* (DE GRAAFF 1981). *G. paeba* occupies areas of allopatry, but also occurs sympatrically with *G. vallinus* and *G. setzeri*, and syntopically with *G. tytonis* locally and seasonally (BOYER 1987; ERASMUS, in litt.; DEMPSTER, PERRIN and DOWNS pers. obs.).

Gerbillurus species lack a ventral gland, as occurs in *M. unguiculatus* and *M. hurrianae* (BROWN 1985; PRAKASH et al. 1988). The only glands found in the skin of *G. paeba* were on the naked toe-pads of fore- and hindfeet (GREEN 1988). Scentmarking behaviour in the form of perineal dragging occurs rarely (DEMPSTER pers. obs.). All *Gerbillurus* species sandbathe by rolling rapidly from the side to the dorsum (DEMPSTER pers. obs.). *G. paeba* and *G. tytonis* selected fine dusty sand for sandbathing in preference to coarser grades of sand (HAMER 1985). *Gerbillurus* spp. maintained in laboratory cages are remarkably odourless to humans except for *G. tytonis* individuals, whose odour is distinctive (DEMPSTER pers. obs.).

In the present study, olfactory preferences of males and females were tested using odours of the opposite sex in each test combination. Tests in which animals were prevented from contacting the odour source were compared with tests in which contact was permitted. In addition, male preferences for odours of females in artificially-induced oestrus were tested.

Materials and methods

Details of numbers of individuals, sexes, and trap localities are given in Table 1. Laboratory maintenance of animals is described elsewhere (DEMPSTER and PERRIN 1989b). The choice chamber used in tests of olfactory preference is illustrated in Figure 1.

All tests were of the heterosexual type, i.e. if males were the odour sources, females were test animals and vice versa. A test animal was placed in the central arena and permitted to investigate the apparatus for 5 min. In the following 15 min, the animal's visits to and time spent in each tunnel were recorded using a programmed microprocessor. After each observation, the whole apparatus was

Table 1. Number of individuals, sexes and trap localities of gerbils used in olfactory preference experiments

Species	Sex	N	Trap locality
<i>G. paeba</i>	Males	11	Swakopmund, Namibia
	Females	16	Swakopmund, Namibia
	Males	9	Kuiseb River, Namibia
	Females	7	Kuiseb River, Namibia
<i>G. tytonis</i>	Males	12	Namib dunefield
	Females	18	Namib dunefield
<i>G. setzeri</i>	Males	5	Arandis, Namibia
	Females	5	Arandis, Namibia
	Males	9	Gobabeb, Namibia
	Females	9	Gobabeb, Namibia
	Males	8	Donkerhoek, Namibia
	Females	1	Donkerhoek, Namibia
<i>G. vallinus</i>	Males	14	Kenhardt, N. Cape
	Females	11	Kenhardt, N. Cape

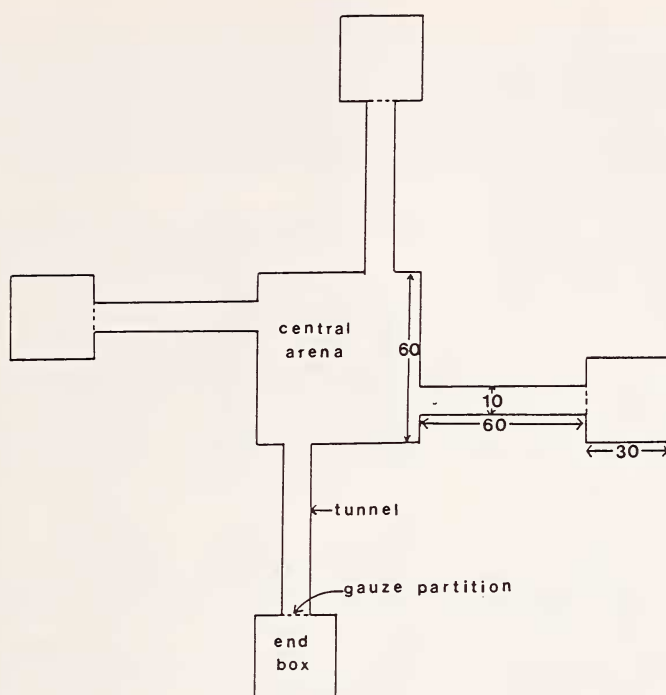


Fig. 1. Choice chamber used in olfactory preference tests. Measurements are given in cm

washed out with odourless soap and water. The allocation of odour source to tunnel was changed on each day of testing.

Observations were conducted in a quiet, window-less room, with lighting provided by a single red light positioned above the centre of the apparatus. Two animals of each species, i.e. eight individuals, were tested on each day of testing, and tests were conducted at weekly intervals.

Three experimental procedures were followed:

Experiment I: Clean sand was placed in each of the end boxes. Four animals of the same sex, but of different species, were placed singly in the end boxes for 18 h, after which they were removed and testing as described above commenced.

Experiment II: Sand from the cages of four individuals of the same sex, but of different species, was used as the odour source. Animals had been housed singly in cages for at least one week prior to testing. A glass petrie dish containing 20 ml of sand was placed approximately 5 cm inside the entrance to each tunnel. The sand was changed after each observation.

Experiment III: The choice chamber was divided in half by a metal partition. Four animals of the same sex and of different species were placed in containers which held 250 ml clean sand. After 1 h the animals were removed and the containers sealed. A glass petrie dish containing 20 ml of this sand was placed approximately 5 cm inside the entrance to each tunnel. The sand was changed after each observation. Two-way tests of *G. vallinus*-*G. setzeri* and *G. paeba*-*G. tytonis* combinations were conducted.

The oestrus condition of females was not considered in these experiments, since vaginal smears were not reliable indicators of the oestrus cycle in *Gerbillurus* species (DEMPSTER and PERRIN 1989b). One set of observations in Experiment I used as odour sources females of all species which had been injected with 0.006 mg oestradiol-17B and 0.4 mg progesterone to induce oestrus.

Results of four-way choice experiments were analysed using Friedman's 2-way analysis of variance with correction for tied ranks (ZAR 1974). Wilcoxon T-test (one-tailed) was used to test the hypothesis that each species preferred conspecific odours in Experiment III.

Results

Results for animals that visited less than two tunnels in the entire observation period were discarded. This accounted for 15 % of all observations. The number of visits made and the time spent in each tunnel varied considerably among individuals. Results for number of visits are presented in Tables 2 to 4, while results for duration of visits are presented as box-and-whisker plots (STATGRAPHICS) in Figs. 2-4.

Table 2. Mean ($\pm$ s.d.) number of visits to odours of different species in Experiment I

Test Animal	n	Odour sources				Friedman's X^2
		<i>G. vullinus</i>	<i>G. setzeri</i>	<i>G. paeba</i>	<i>G. tytonis</i>	
Males		Females				
<i>G. vullinus</i>	18	13.4 $\pm$ 13.6	11.3 $\pm$ 8.6	15.4 $\pm$ 12.5	10.8 $\pm$ 9.1	6.7 n.s.
<i>G. setzeri</i>	17	8.8 $\pm$ 4.0	9.1 $\pm$ 3.8	8.5 $\pm$ 5.4	8.8 $\pm$ 4.7	1.8 n.s.
<i>G. tytonis</i>	18	7.1 $\pm$ 4.4	9.2 $\pm$ 4.6	7.3 $\pm$ 3.6	8.9 $\pm$ 3.9	7.2 n.s.
<i>G. paeba</i>	18	12.9 $\pm$ 18.5	13.2 $\pm$ 15.8	13.3 $\pm$ 11.9	7.3 $\pm$ 7.1	3.6 n.s.
Females		Males				
<i>G. vullinus</i>	15	15.8 $\pm$ 23.3	13.1 $\pm$ 18.9	11.5 $\pm$ 16.4	10.9 $\pm$ 19.3	4.5 n.s.
<i>G. setzeri</i>	15	11.5 $\pm$ 5.4	11.6 $\pm$ 5.4	10.9 $\pm$ 3.9	10.2 $\pm$ 3.8	1.9 n.s.
<i>G. tytonis</i>	15	7.9 $\pm$ 3.9	9.6 $\pm$ 5.6	10.6 $\pm$ 6.3	8.3 $\pm$ 5.8	7.6 n.s.
<i>G. paeba</i>	13	11.1 $\pm$ 7.8	12.6 $\pm$ 9.7	13.1 $\pm$ 11.9	10.9 $\pm$ 10.7	2.3 n.s.

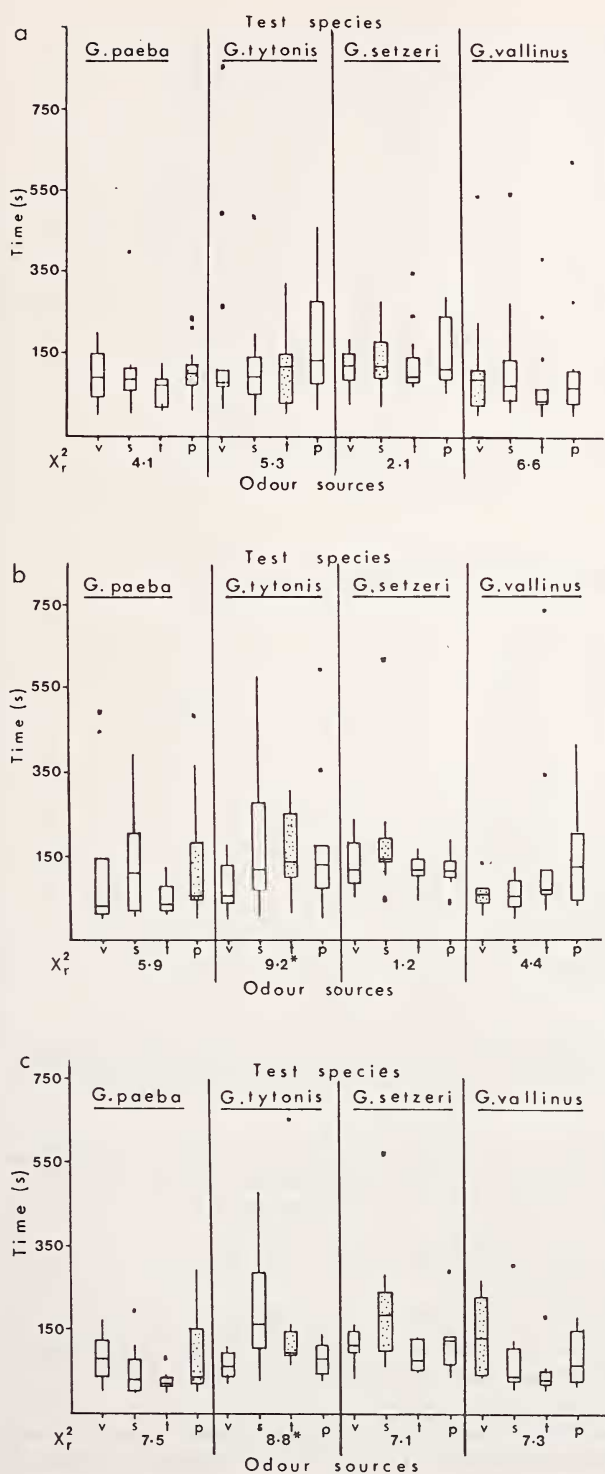
Table 3. Mean ($\pm$ s.d.) number of visits to odours of different species in Experiment II

Test Animal	n	Odour sources				Friedman's X^2
		<i>G. vullinus</i>	<i>G. setzeri</i>	<i>G. paeba</i>	<i>G. tytonis</i>	
Males		Females				
<i>G. tytonis</i>	10	6.8 $\pm$ 4.1	8.2 $\pm$ 4.5	12.5 $\pm$ 12.6	11.6 $\pm$ 14.1	0.8 n.s.
<i>G. paeba</i>	10	21.4 $\pm$ 19.1	19.7 $\pm$ 26.6	22.7 $\pm$ 25.2	22.7 $\pm$ 26.7	0.4 n.s.
<i>G. setzeri</i>	10	10.2 $\pm$ 4.4	10.1 $\pm$ 8.1	11.1 $\pm$ 10.4	9.7 $\pm$ 11.7	0.8 n.s.
<i>G. vullinus</i>	10	7.7 $\pm$ 6.7	6.3 $\pm$ 4.7	5.1 $\pm$ 4.5	5.5 $\pm$ 3.5	0.7 n.s.
Females		Males				
<i>G. tytonis</i>	10	10.6 $\pm$ 7.0	9.8 $\pm$ 4.4	7.5 $\pm$ 3.3	9.5 $\pm$ 4.1	2.0 n.s.
<i>G. paeba</i>	10	15.9 $\pm$ 18.9	12.6 $\pm$ 11.9	14.8 $\pm$ 17.8	12.5 $\pm$ 17.8	0.2 n.s.
<i>G. setzeri</i>	10	11.5 $\pm$ 6.0	12.5 $\pm$ 6.7	10.5 $\pm$ 5.9	12.0 $\pm$ 10.7	3.6 n.s.
<i>G. vullinus</i>	10	4.8 $\pm$ 3.9	4.8 $\pm$ 3.4	6.0 $\pm$ 3.5	7.0 $\pm$ 6.0	2.8 n.s.

Table 4. Mean ($\pm$ s.d.) number of visits to odours of different species in Experiment III

Test Animal	n	Odour sources				Wilcoxon T
		<i>G. tytonis</i>	<i>G. paeba</i>	<i>G. vullinus</i>	<i>G. setzeri</i>	
Males		Females				
<i>G. tytonis</i>	10	20.5 $\pm$ 15.0	18.2 $\pm$ 20.9			24.5 n.s.
<i>G. paeba</i>	10	24.9 $\pm$ 24.8	11.0 $\pm$ 10.8			19.0 n.s.
<i>G. setzeri</i>	10			29.7 $\pm$ 37.3	35.9 $\pm$ 42.2	21.0 n.s.
<i>G. vullinus</i>	10			11.5 $\pm$ 9.6	16.7 $\pm$ 18.7	10.0 n.s.
Females		Males				
<i>G. tytonis</i>	10	23.3 $\pm$ 9.7	19.3 $\pm$ 7.5			2.0*
<i>G. paeba</i>	10	14.2 $\pm$ 7.8	26.3 $\pm$ 27.3			24.5 n.s.
<i>G. setzeri</i>	9			14.9 $\pm$ 10.8	12.2 $\pm$ 5.6	5.0*
<i>G. vullinus</i>	9			25.2 $\pm$ 21.0	18.6 $\pm$ 11.6	8.0*

* = $p \leq 0.05$



Results of Experiment I are given in Table 2 and Figure 2. Number of visits to odours of different species did not differ significantly in any species or sex. *G. tytonis* males and females and *G. vullinus* males were nearest to significance at the 95 % probability level, but in no case did this indicate a greater number of visits to conspecific odours.

Durations of visits differed significantly in only two test situations. Male *G. tytonis* spent more time with conspecific odour of injected females and avoided *G. vullinus* odour. However, for untreated females, male *G. tytonis* preferred the odour of *G. setzeri* and, avoided *G. vullinus* and *G. paeba*. Males discriminated more among untreated females than among injected females, and two species, *G. vullinus* and *G. setzeri*, preferred conspecific to hetero-specific odours. X^2_r values for these tests approached significance at the 95 % probability level. *G. tytonis* odours were avoided by all species except *G. tytonis* males.

Female *G. vullinus* were the only species which showed a preference for male conspecific odours, but differences were not significant.

Fig. 2. Durations of visits made by a) females to odours of males ($n = 13$ for *G. paeba*, $n = 15$ for other species); b) males to odours of treated females ($n = 10$ for each species); c) males to odours of untreated females ($n = 8$ for each species). * = $p < 0.05$; all other X^2_r values not significant

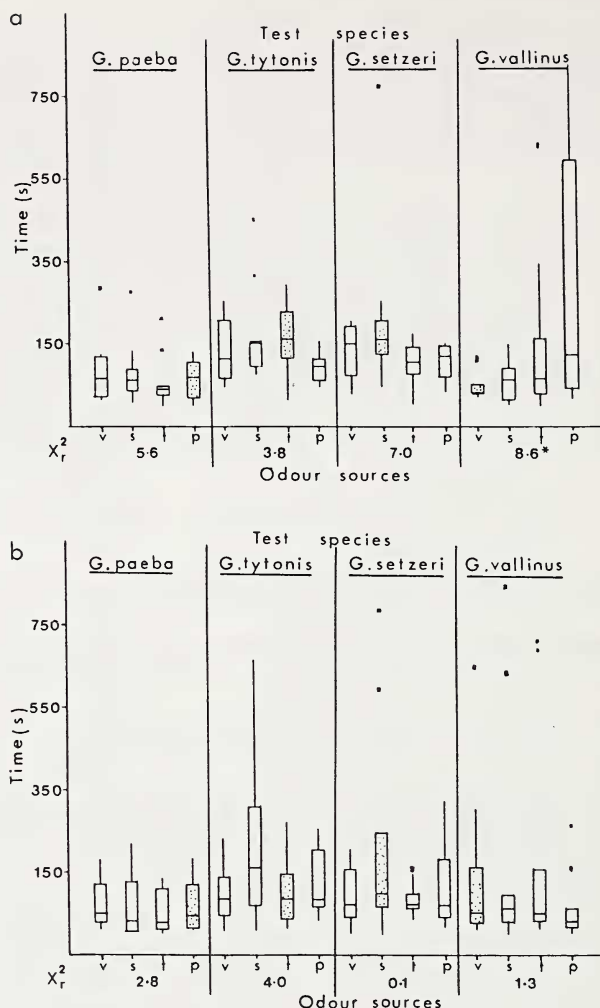


Fig. 3. Durations of visits made by a) females to odours of males ($n = 10$ for each species); b) males to odours of females ($n = 10$ for each species). * = $p < 0.05$; all other χ^2 values not significant

Results of Experiment II are shown in Fig. 3 a) and b) and Table 3. Numbers of visits to different odours did not differ significantly in any species or sex, and high probability values were calculated in all tests. Durations of visits varied significantly in only one species; *G. vallinus* females avoided conspecific odours and preferred male *G. paeba* odours. Female *G. setzeri* preferred conspecific odours, and this result approached significance at the 95 % probability level.

Results of Experiment III are shown in Fig. 4 a) and b) and Table 4. No significant differences were noted in the number of visits made to female odours by males. *G. setzeri* males spent more time near conspecific odours, but differences for this and other species were not significant.

Female *G. setzeri* visited male *G. vallinus* odours significantly more frequently than male *G. setzeri* odours, but durations of visits were not significantly different. *G. vallinus*

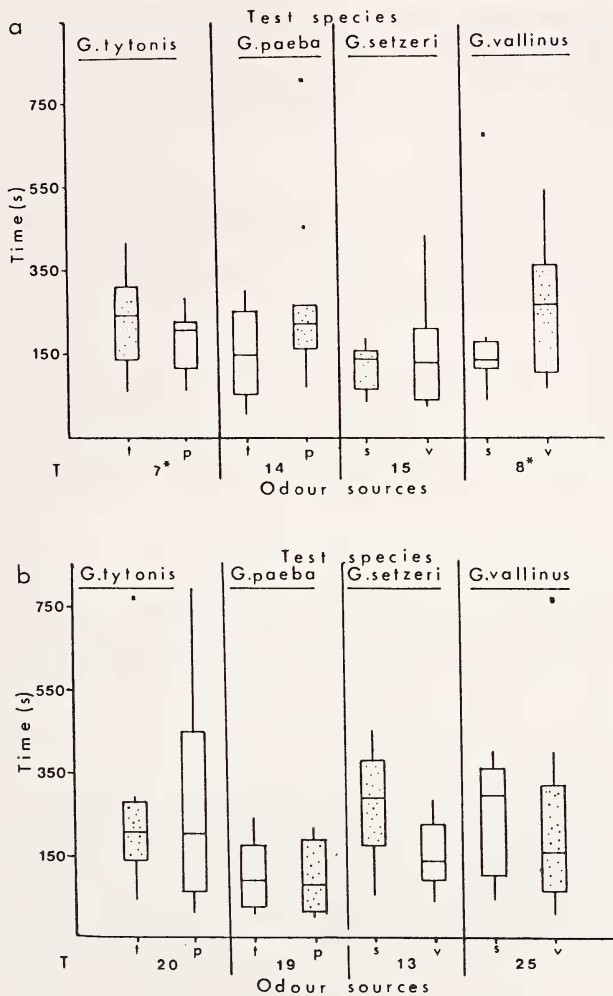


Fig. 4. Durations of visits made by a) females to odours of males ($n = 9$ for *G. vallinus* and *G. setzeri*, $n = 10$ for *G. paeba* and *G. tytonis*); b) males to odours of females ($n = 10$ for all species). * = $p \leq 0.05$, all other T values not significant

and *G. tytonis* females visited conspecific odours significantly more frequently and for a longer time than heterospecific odours. Female *G. paeba* preferred conspecific odours, but this difference was not significant.

Discussion

Male *Gerbillurus* spp. showed more discrimination when they were prevented from making contact with the odour source, while females showed more discrimination when they were able to make contact with the odour source. Sexual dimorphism of odours is indicated by these results, as occurs in other rodent species (Nyby 1982). Male rats demonstrated a preference for odours of oestrus females over dioestrus females, but this preference disappeared when males were allowed physical contact with the odour source.

A similar effect occurred in mice and hamsters, and may partially account for differing results obtained by different researchers (NYBY 1982).

NYBY (1982) has suggested that a volatile chemosignal which serves as a long-range sex attractant is produced by several female rodent species; male response to this signal is dependent on previous sexual experience. For *Gerbillurus* species, a volatile chemosignal of females appears to exist.

Male *Gerbillurus* spp. discriminated less clearly among odours of oestrus-induced females than among untreated female odours. Artificial induction of oestrus in female *Gerbillurus* rarely resulted in copulatory behaviour, although 80 % of females had vaginal smears which were devoid of leucocytes after hormone treatment (DEMPSTER and PERRIN 1989b). The lack of response of male *Gerbillurus* may have been due to failure to induce oestrus effectively.

Response to the volatile chemosignal of oestrus female rats, mice, and hamsters appears to be dependent on prior sexual experience of males (NYBY 1982). Animals used in this study were wild-caught as adults and rarely bred in captivity (DEMPSTER and PERRIN 1989b). Thus, lack of sexual experience may have contributed to the present results. However, male *Dipodomys merriami* and *M. unguiculatus* did not prefer the odour of urine from oestrus or prooestrous females to that of non-oestrus females (GREGG and THIESSEN 1981; RANDALL 1983).

Male odours accelerate puberty in juvenile female rodents of a number of species (BROWN 1985). Oestrus female *D. merriami* (RANDALL 1983) and *M. unguiculatus* (GREGG and THIESSEN 1981) preferred urine of intact males to that of castrated males, and oestrus female *Spalax ehrenbergi* preferred homochromosomal odours of cage litter or urine (NEVO et al. 1976). In *Gerbillurus* species, females were more discriminating if they were permitted to make contact with the odour source, indicating that they were responding to non-volatile chemosignals. However, few results were statistically significant. The oestrous condition of female *Gerbillurus* may have influenced the present results. Anoestrus female *S. ehrenbergi* did not discriminate among male odours (NEVO et al. 1976). Oestrus female *D. merriami* (RANDALL 1982) and *M. unguiculatus* (GREGG and THIESSEN 1981) showed greater response to intact male urine than did anoestrus females.

Although discrimination as measured by time occurred in a few species, this did not always indicate a preference for the odour of conspecifics. Males preferred conspecific odours in 6/16 test situations, and females preferred conspecific odours in 6/12 test situations, but differences were significant in only 3/28 test situations. Male *G. tytonis* preferred injected conspecific odours in Experiment I; female *G. vallinus* and *G. tytonis* preferred conspecific odours in Experiment. III. Other significant results were ambiguous: female *G. vallinus* preferred male *G. paeba* and avoided conspecific odours, male *G. tytonis* preferred untreated female *G. setzeri* odours, and female *G. setzeri* preferred male *G. vallinus* odours in Experiment III.

Results of two-way choice tests were similar to those obtained in Experiment II. Thus lack of detection of olfactory preference was not due to confusion resulting from a testing procedure which was too complex. Using freshly-collected odours in Experiment III also had little effect on the results, indicating that lack of conspecific preference was not due to bacterial decay of chemosignals.

The results presented here negate the hypothesis that *Gerbillurus* species identify conspecifics by response to deposited chemosignals. *Gerbillurus* differed considerably from some other rodent species, which differentiated among odours of individuals (JOHNSTON 1982; Young 1988). Male bank voles preferred the scent of their own race (GODFREY 1958) and mated preferentially with their own race. House mice, however, did not differentiate among individuals of other populations (PERRIGO and BRONSON 1983). Several studies have investigated olfactory discrimination as a sexual isolating mechanism in *Peromyscus* species and subspecies. Oestrus female *P. maniculatus bairdi* and *P. leucopus*

noveboracensis preferred conspecific male odours (DOTY 1972). MOORE (1965) has suggested that species discrimination of odours has evolved in *P. maniculatus* because of coexistence with other *Peromyscus* species, while no conspecific preference was exhibited by the geographically-isolated *P. polionotus*. Male *P. eremicus* and *P. californicus* from areas of sympatry showed stronger preference for conspecific odours than did allopatric animals (SMITH 1965).

Gerbillurus individuals used in this study were from geographically separated populations. Detailed data on distribution of *Gerbillurus* species is lacking, but areas of sympatry and allopatry do exist (BOYER 1988; ERASMUS in litt.; GRIFFIN in litt.). Results presented here suggest that species discrimination of deposited chemosignals has not evolved in allopatric populations. *Gerbillurus* species produced small volumes of urine (DOWNS and PERRIN pers. obs.) and few sudoriferous glands were found in the skin of *G. paeba* (GREEN 1988). Nasonasal sniffing was frequently observed in staged male-female encounters; anogenital sniffing occurred more rarely (DEMPSTER 1986). RANDALL (1982) reported that male *D. merriami* were attracted to the vaginal odour of oestrus females, but needed to actually sniff the female's vaginal area before responding. The present results suggest that deposited chemosignals play a limited role in species discrimination in *Gerbillurus* species; physical contact with a potential mate may be necessary.

Acknowledgements

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Zusammenfassung

Zwischenartliche Geruchsunterscheidung bei vier Gerbillurus-Arten

Die geruchliche Unterscheidung zwischen Angehörigen der vier Arten der Gattung *Gerbillurus* wurde bei Männchen und Weibchen aller dieser Arten untersucht. In Vierfachwahlversuchen konnte sich jedes Versuchstier für den Geruch eines Tieres des entgegengesetzten Geschlechts von *G. paeba*, *G. tytonis*, *G. setzeri* oder *G. vallinus* entscheiden. Hatten die Versuchstiere keinen Zugang unmittelbar zur Geruchsquelle (imprägniertem Sand), unterschieden die Männchen deutlicher als die Weibchen. Aber nur männliche *G. tytonis* bevorzugten signifikant den Geruch konspezifischer Weibchen. Die Männchen unterschieden weniger deutlich zwischen Weibchen, die hormonell behandelt worden waren, um bei ihnen Oestrus zu induzieren.

Durften die Versuchstiere die Duftquelle berühren, unterschieden die Weibchen deutlicher in Zweifach- als in Vierfachwahlen. Im Zweifachwahlverfahren bevorzugten weibliche *G. tytonis* und *G. vallinus* signifikant art eigene Gerüche.

Vermutlich reagieren die Männchen auf flüchtige Duftstoffe der Weibchen, unterscheiden aber weniger deutlich, wenn sie die Duftquelle beriechen können. Die Weibchen reagierten auf nicht flüchtige, von den Männchen abgegebene chemische Signale, zeigten aber kaum eine Bevorzugung der Gerüche von Artgenossen. Der physische Kontakt zwischen den Tieren ist vermutlich zum sicheren Erkennen des Artgenossen notwendig.

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